

British Carboniferous Edrioasteroidea (Echinodermata)

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Synopsis

The entire British fauna of Carboniferous edrioasteroids is revised and redescribed and a newly discovered hardground, where edrioasteroids are exceedingly abundant, is described. All belong to the family Agelacrinitidae and three genera and four species are recognized. Two of the genera, *Lepidodiscus* and *Postibulla*, are known from North America but the third, *Stalticodiscus* (type species *Lepidodiscus milleri*), is new. The new species *Postibulla neglecta* is described. Growth and plate ultrastructure of *Stalticodiscus milleri* have been studied using scanning electron microscopy. This species was able to orientate itself in currents and possibly lived in bimodal (i.e. tidal) current regimes with the anterior-posterior axis at right angles to the flow of water.

Introduction

It is now more than a hundred years since the first edrioasteroid was described from the Carboniferous of the British Isles, yet they have remained extremely rare fossils known from only a few localities in northern England. Three species have been described with varying accuracy, *Lepidodiscus lebouri* Sladen 1879, *Lepidodiscus milleri* Sharman & Newton 1892 and *Lepidodiscus fistulosus* Anderson 1939. This last species was thought so distinct that Regnéll (1950) erected the genus *Anglidiscus* for it.

The only edrioasteroids known from the Carboniferous are isorophids belonging to the family Agelacrinitidae. These, like all isorophids, were sessile and lived attached to hard substrates. Only the upper (ventral) surface is calcified and the skeleton consists of imbricate or tessellate plates set within a soft tissue membrane. Upon death, the theca rapidly dissociates as the soft tissue decays and so, to be preserved, edrioasteroids must be buried alive or within a very short time of death. However, isorophids lived on hard substrates in areas of active erosion where they stood very little chance of being preserved. It is therefore only under exceptional circumstances that we ever find them in the fossil record. Until now, most specimens found in the British Carboniferous have been single individuals attached to shells, presumably living at the limits of tolerance offshore to the main population. The discovery of a new horizon in the Lower Carboniferous of Cumbria yielding an abundance of well-preserved edrioasteroids is an unusual and important find and I am extremely grateful to Dr Paul Taylor of the British Museum (Natural History) who brought this occurrence to my notice.

The discovery prompted a re-examination of the previously-described species, and it soon became apparent that published descriptions were unsatisfactory. The contemporary American fauna is now well known from the work of Bassler (1936), Kesling (1960) and especially Bell (1976a). This paper sets out to revise the British Carboniferous edrioasteroids.

Occurrence

All the British Carboniferous edrioasteroids come from the Early Asbian stage of the Dinantian. American Carboniferous edrioasteroids have been discovered at various levels throughout the Mississippian and it is not at all clear why the British fauna should be so restricted in its occurrence. There are five localities that have yielded edrioasteroids, all of them in

northern England. I am indebted to Dr W. H. C. Ramsbottom of the Institute of Geological Sciences, Leeds, who supplied me with accurate stratigraphic data on these localities, as follows.

(i) The River Irthing, one mile (1.6 km) east of Waterhead, Northumberland (National Grid reference (approx.) NY 635685). This occurrence was reported by Sharman & Newton (1892) and Ramsbottom (1970: 172). Here the Millerhill Limestone outcrops as a strike section for some distance. This limestone is divided into an upper and a lower unit but it is not known from which of these the single edrioasteroid came. The Millerhill Limestone lies within the Upper Border Group and is middle Early Asbian in age. One specimen of *Stalticodiscus milleri* (Sharman & Newton) has been collected from here.

(ii) The River Irthing, $\frac{5}{8}$ of a mile (1 km) south of Lampert, Northumberland at the foot of Linen Sike (NY 683735). A specimen of *Stalticodiscus milleri* (Sharman & Newton) has been found here in a shelly calcareous shale that lies just above the Millerhill Limestone. This is again middle Early Asbian in age. It was recorded by Sharman & Newton (1892) and Ramsbottom (1970: 172).

(iii) A horizon 103 ft 6 in (31.5 m) down the Hetton House borehole (NU 042296) yielded some 33 edrioasteroids (Anderson 1939). These come from a siltstone with calcareous bands situated about half way up the Scremerston Coal Group and Early Asbian in age, probably not very far from the Millerhouse Limestone horizon. The fauna consists mainly of *Lepidodiscus* cf. *squamosus* Meek & Worthen with subsidiary *Postibulla neglecta*.

(iv) An impure limestone outcropping in the River Rede, where it forms a low waterfall just north of the bridge above the village of East Woodburn, Northumberland (NY 901877). Here was found the only known specimen of *Lepidodiscus lebouri* Sladen (Sladen 1879; Miller 1887: 41). This horizon is approximately 900 ft (275 m) below the Redesdale Limestone (not 700 ft as stated by Miller) and lies close to the top of the Early Asbian.

(v) The road cutting at Penruddock on the north side of the A66 road just at the end of a stretch of dual carriageway some 6 miles (9.5 km) west of Penrith, Cumbria (NY 438275). The succession here is given in Fig. 1. Edrioasteroids occur crowded on the upper surfaces of bored and encrusted micritic concretions which can be several feet in diameter. This horizon had obviously been exposed for a considerable time before being smothered by a rapid influx of mud. In general the encrusting bryozoa and inarticulate brachiopods are found on the undersides of the concretions whereas acrothoracic barnacle borings and edrioasteroids are found on the upper surfaces. Concretions with abundant borings tend not to have edrioasteroids and *vice versa*.

The brachiopods from this locality suggest an Asbian age, according to Dr C. H. C. Brunton of the BM(NH) (personal communication). The foraminifera, which include *Koninckopora inflata* (de Koninck), *Eostaffella parastruvei* Rauser, *Archaeodiscus* sp. and *Globoendothyra*, were identified by Dr A. R. E. Strank of the I.G.S., Leeds, and indicate a Holkerian or Early Asbian age. Dr W. H. C. Ramsbottom informs me that the beds at this locality probably belong to the undivided Sixth/Seventh Limestones, in the lower part of the Early Asbian.

Taxonomy

Order ISOROPHIDA Bell, 1976

Suborder ISOROPHINA Bell, 1976

Family AGELACRINITIDAE Chapman, 1860

Genus *LEPIDODISCUS* Meek & Worthen, 1868

[= *Angliscus* Regnéll, 1950]

Lepidodiscus cf. *squamosus* Meek & Worthen, 1868

Figs 2–5, 8

1868 *Agelacrinites* (*Lepidodiscus*) *squamosus* Meek & Worthen: 357–358.

1939 *Lepidodiscus fistulosus* Anderson: 68 (part).

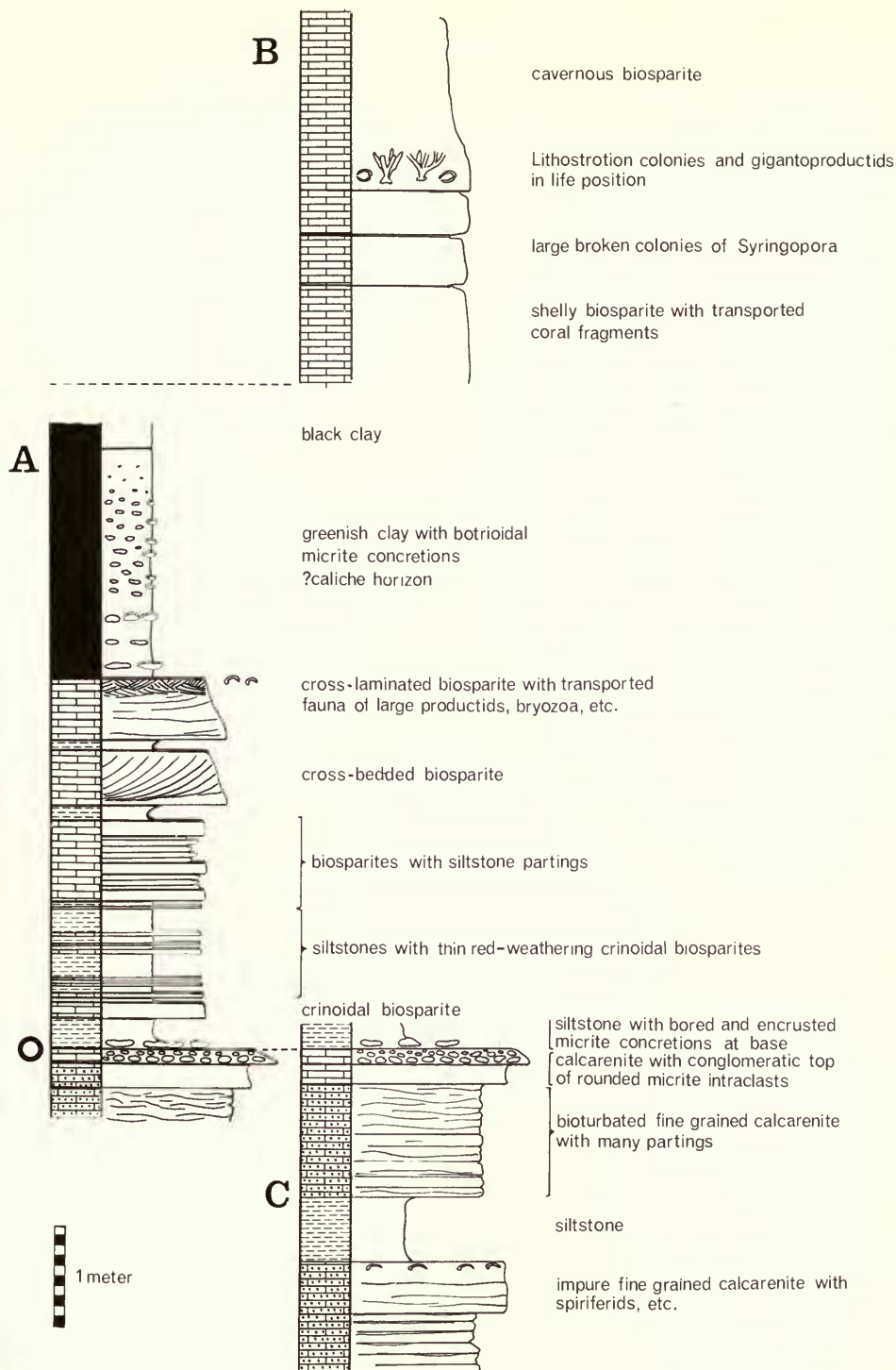
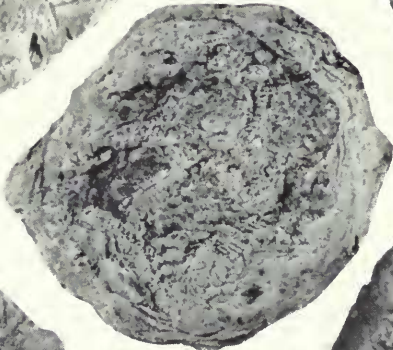


Fig. 1 Sedimentary log for succession exposed at Penruddock road cutting, near Penrith (loc. v). A, succession towards the west end of the road cutting. B, succession in the old quarry immediately above the road cutting. C, succession towards the east end of the road cutting, east of the an obvious fault. O – the horizon with edrioasteroids encrusting limestone concretions.



1950 *Angliscus fistulosus* (Anderson); Regnéll: 6 (part).

1966 *Angliscus fistulosus* (Anderson); Regnéll: U162 (part).

1976a *Lepidodiscus squamosus* Meek & Worthen; Bell: 253–257 (q.v. for full bibliography of American records).

DIAGNOSIS. An agelacrinitid with a clavate theca and long curved ambulacra. Ambulacra I–IV curve sinistrally, V curves dextrally (rarely all curve sinistrally). Cover plates arranged cyclically in groups of six or seven. Oral area composed of many cover plates continuous with ambulacral series. Hydropore rise in posterior right of oral area (type VI of Kesling, 1960), posterior side formed of many plates. Interambulacral plates squamose, imbricate. Periproct an anal valve of two cycles of plates. Flooring plates uniserial, imbricate.

MATERIAL. Institute of Geological Sciences no. 60235. Half of a six-inch (150 mm) core with parts of 31 specimens.

LOCATION AND AGE. Hetton House bore-hole, Northumberland (loc. iii, p. 114). Early Asbian, Dinantian.

DESCRIPTION. The British specimens of this species all come from one piece of bore-hole core. There are parts of 31 specimens of which only 15 are tolerably complete. A further two specimens belong to the genus *Postibulla* and are described later. All the specimens are preserved upside down, revealing the inner surface of the theca. Latex moulds were made of three of the better-preserved specimens.

In life the specimens must have been tall and domal in shape but most are preserved in the contracted state. In all but one specimen ambulacra I–IV curve sinistrally and ambulacrum V curves dextrally. There is, however, one (? abnormal) specimen in which all five ambulacra curve sinistrally (Fig. 8). Distally the ambulacra curve round to become parallel to the periphery. The arrangement of cover plates is nowhere clear but cycles of three or four large plates together with small intercalated plates can be seen. This seems comparable with the cyclical cover plate arrangement seen in the better-preserved American material. Ambulacral flooring plates are uniserial and imbricate. Contrary to Anderson's (1939) findings, the flooring plates are totally imperforate. Preservation around the oral area is too poor to permit a detailed analysis of the cover plate arrangement but it is clear that the oral cover plates are continuous with the ambulacral cover plates and that no enlarged oral primary cover plates are present. Oral cover plates are numerous and small. There is a prominent hydropore bulge situated to the posterior of the oral area adjacent to ambulacrum V. The posterior side of this bulge is formed by a number of small plates.

Interambulacral areas are composed of numerous squamose, imbricate plates that become noticeably smaller towards the ambulacra and around the anal cone. The inner surface of these plates is composed of a coarse-meshed stereom which led Anderson (1939) to believe mistakenly that they were perforate. The anal cone lies roughly central in interambulacrum 5 and consists of a double circlet of rather elongate triangular plates. The peripheral rim is of standard appearance.

Figs 2–6 IGS no. 60235, the half core from which Anderson described *Lepidodiscus fistulosus*. Fig. 2, the whole specimen, $\times 0.8$; L = lectotype of *Angliscus fistulosus* (= *Lepidodiscus* cf. *squamosus*) (see Fig. 4), P = holotype of *Postibulla neglecta* sp. nov. (see Fig. 6). Fig. 3, *Lepidodiscus* cf. *squamosus* Meek & Worthen, latex cast of specimen xxix of Anderson (1939: 70) situated to the lower right of the letter P in Fig. 2, $\times 4$. Fig. 4, *Lepidodiscus* cf. *squamosus* Meek & Worthen, natural mould, **lectotype** of *Angliscus fistulosus* (Anderson) (L in Fig. 2), $\times 4$. Fig. 5, *Lepidodiscus* cf. *squamosus* Meek & Worthen, latex cast of specimen xxii of Anderson (1939: 70), an abnormal individual with all five arms curving sinistrally, $\times 4$; see Fig. 8. Fig. 6, *Postibulla neglecta* sp. nov., **holotype** (P in Fig. 2), number xxvi of Anderson (1939: 70), $\times 4$; see Fig. 11.

Fig. 7 *Lepidodiscus lebouri* Sladen, BM(NH) E29330, holotype $\times 2\frac{1}{2}$. See Fig. 9.

Figs 2–7 whitened with ammonium chloride sublimate.

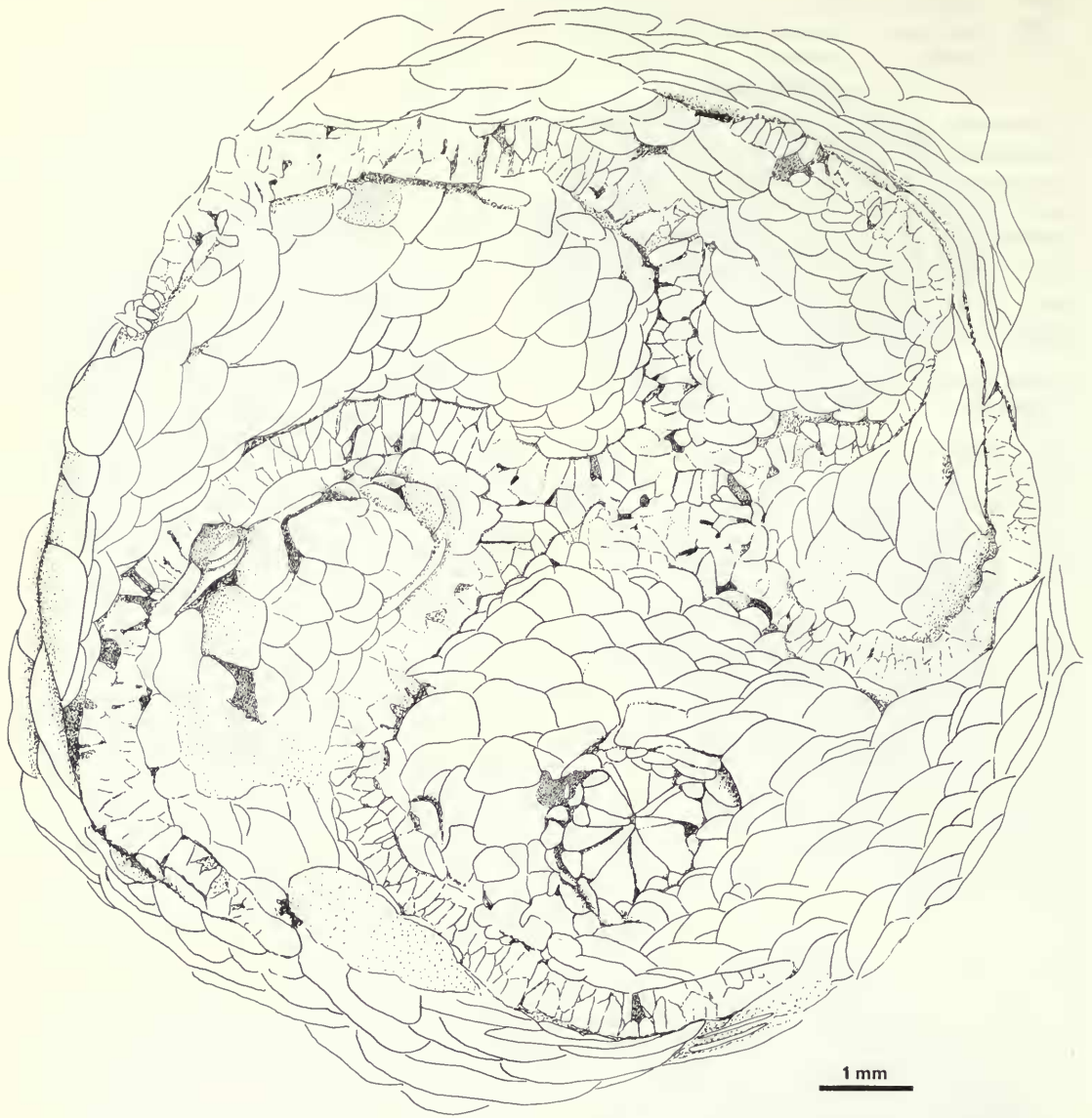


Fig. 8 *Lepidodiscus* cf. *squamosus* Meek & Worthen. Camera-lucida drawing of Anderson's specimen xxii (IGS no. 60235), an abnormal individual with all five arms curving sinistrally. See Fig. 5.

DISCUSSION. One rather unusual feature of this material is that the specimens are preserved in a siltstone with thin calcareous bands. They are not all preserved on one level but are present at two levels a few millimetres apart. It is obvious that the sediment was not lithified into a hard ground at this horizon and that the edrioasteroids were not attached to the sediment, since they have all separated to reveal their inner surfaces. The most likely explanation for this is that the edrioasteroids were originally attached to one or more fronds of free-standing alga which became detached and transported before being rapidly buried. Decay of the alga left the edrioasteroids buried without trace of the substratum to which they were attached.

The fact that the specimens only show the inner surface of their thecal plating, together with the rather poor state of preservation, makes the interpretation of their structure difficult. This probably explains why Anderson's (1939) original description contains a number of basic misconceptions. No holotype of *Lepidodiscus fistulosus* was designated by Anderson and only a general reconstruction was given. However, as Anderson's reconstruction was supposedly based mainly on his specimen (1939: 70) viii, this is here designated the **lectotype**. Anderson believed that all the edrioasteroids on this block belonged to *L. fistulosus*, but although most individuals, including the lectotype, are here referred to *Lepidodiscus* cf. *squamosus*, two belong to the genus *Postibulla*. There is no evidence that the flooring plates are pierced by pores, nor can I find the purported median groove on the flooring plates. More importantly, the oral plating arrangement shown in Anderson's reconstruction is incorrect. Anderson (1939: 78–79) assumed that 'the mouth . . . is covered by three peristomal plates as in *A(gelacrinites) pileus* Hall, though only the posterior one can be recognized'. I can only think that he mistook the large hydropore plate seen in one of the specimens of *Postibulla* for the posterior primary oral cover plate (Fig. 11, p. 122). The reconstructed arrangement of ambulacral cover plates is also incorrect.

Lepidodiscus fistulosus was referred to the family Hemicystitidae by Regnéll (1950), who created the new genus *Anglidiscus* for it. He did this on the strength of Anderson's description and without having seen the original specimens. As the species is synonymous with *Lepidodiscus squamosus*, *Anglidiscus* is a junior synonym for *Lepidodiscus*.

In America, *Lepidodiscus squamosus* is known from Indiana and Pennsylvania in beds of the Kinderhookian and Osagean Series (Bell 1976a) which pre-date the British find (George *et al.* 1976). There *Lepidodiscus* is a fairly long-ranged genus occurring throughout the Mississippian. *L. squamosus* differs from all other species referred to this genus in having imbricate rather than abutting flooring plates. Compared with American material, in the British specimens of *L. cf. squamosus* the imbrication of the flooring plates is slightly less pronounced and there is somewhat less of an overlap of the two posterior ambulacra behind the periproct. Otherwise the two are comparable as far as can be made out.

The one specimen in which all five ambulacra curve in the same direction (Fig. 8) is in all other respects identical to the remaining specimens of *L. cf. squamosus*. It is clearly just an abnormal individual within the population.

Lepidodiscus lebouri Sladen, 1879

Figs 7, 9, 10

1876 *Agelacrinites (Lepidodiscus) squamosus* Meek & Worthen; Lebour: 22.

1879 *Lepidodiscus lebouri* Sladen: 745; pl. 37, figs 1–4.

1936 *Lepidodiscus lebouri* (Sladen); Bassler: 20; pl. 1, fig. 19.

MATERIAL. Holotype and only known specimen British Museum (Natural History) Palaeontology Dept. no. E29330.

LOCATION AND AGE. From the River Rede near East Woodburn, Northumberland (loc. iv, p. 114). Early Asbian, towards the top of the sub-stage.

DIAGNOSIS. Large clavate species of *Lepidodiscus* with long, curved ambulacra: ambulacra I–IV curve sinistrally, ambulacrum V curves dextrally. Cover plates arranged in cycles of six. Anal cone lies in interambulacrum 5 close to ambulacrum I and is bordered distally by the tip of ambulacrum V. Hydropore included to the posterior right of the oral area, bounded posteriorly by a few small plates. Interambulacra composed of numerous tessellate plates.

DESCRIPTION. There is only one specimen known of this species and it is preserved ventral surface uppermost. Peripherally the plating curves underneath suggesting that in life the theca was clavate in shape. It is a large edrioasteroid with a diameter of 25 mm. There are six

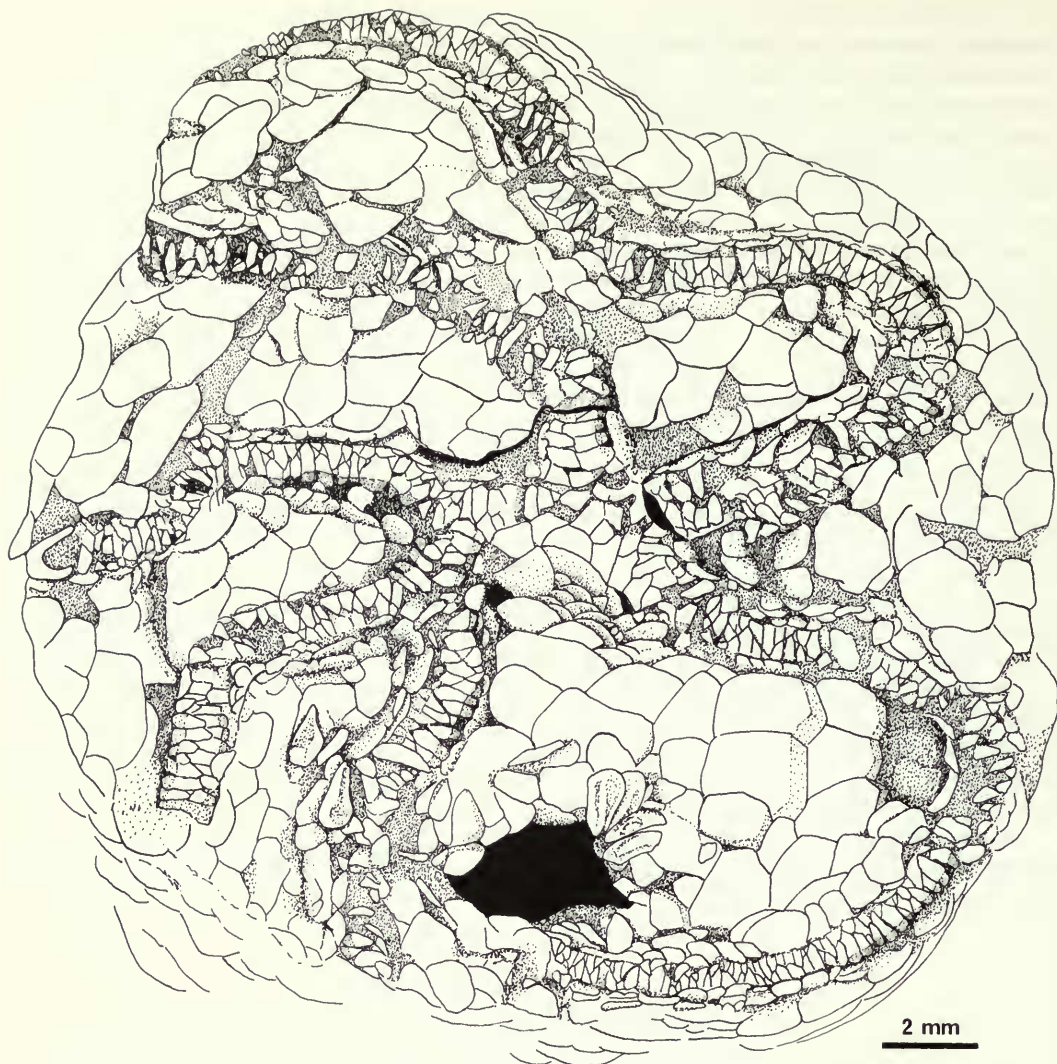


Fig. 9 *Lepidodiscus lebouri* Sladen. Camera-lucida drawing of the holotype BM(NH) no. E29330. See Fig. 7.

ambulacra, an abnormality produced by ambulacrum I bifurcating shortly after it had separated from ambulacrum II. Ambulacrum V curves dextrally; all other ambulacra curve sinistrally. The oral area is covered by a large number of cover plates that are continuous with the ambulacral cover plates. Unfortunately the plating is somewhat disrupted (Fig. 9) and the exact arrangement cannot be determined. There are no distinctly larger primary cover plates. Ambulacral cover plates are arranged in cycles of six, three or four larger plates plus two or three tiny occluded cover plates in each cycle (Fig. 10). The perradial suture is markedly zigzag except over the oral area and the ambulacra form obvious ridges on the theca. Cover plates are small, triangular and wedge-shaped in cross section. The larger cover plates in each cycle have intrathecal extensions. Towards the distal end of the ambulacra the small occluded cover plates are lost from the cycles. Ambulacral flooring plates are largely covered, but can be seen in cross section in ambulacrum II. They are uniserial and U-shaped in cross section.

The hydropore belongs to type VI of Kesling (1960). It lies in the right posterior side of the oral area and is bounded by cover plates anteriorly, and posteriorly by a small number of (?)

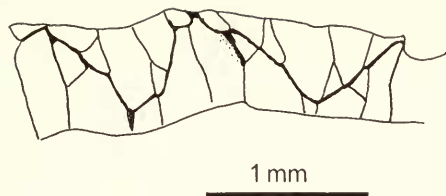


Fig. 10 Camera-lucida drawing of cover plate arrangement from ambulacrum II of the holotype of *Lepidodiscus lebouri* (BM(NH) no. E29330).

interambulacral plates. The posterior slope to the oral area is steep and formed by two rather large plates together with a number of smaller plates (Fig. 9).

Interambulacral areas are broad and composed of numerous sub-polygonal tessellate plates. These are relatively thick and imbricate adorally. The interambulacral plates are largest near the centre of each area but become obviously smaller close to ambulacra and around the periproct.

The periproct is largely disrupted and individual plates of the anal cone lie scattered nearby. It is situated in the more distal left-hand side of interambulacrum 5, fairly close to ambulacrum I. The tip of ambulacrum V curves round to lie just posterior to the periproct.

DISCUSSION. There are three species of *Lepidodiscus* known from North America (Bell 1976a): *L. squamosus* Meek & Worthen, *L. laudoni* (Bassler) and *L. sampsoni* (Miller). *L. lebouri* differs from *L. squamosus* in having tessellate ventral plating and a clavate body. It differs from *L. sampsoni* in having curved ambulacra: the ambulacra in *L. sampsoni* form long, straight ridges on the ventral surface. *L. lebouri* comes closest to the common North American species *L. laudoni*, which is found throughout the Mississippian ranging from the Kinderhookian to the Chesterian. Unfortunately the plating of the pedunculate zone and the internal aspect of the ambulacral flooring plates are unknown for *L. lebouri*. In other features the two species are closely comparable, save for the abnormal sixth ambulacrum in *L. lebouri* and the presence of two prominent plates forming the posterior slope to the oral area. Although *L. lebouri* will probably prove to be conspecific with *L. laudoni*, the two species are here retained as distinct until further British material becomes available for comparison. In uniting the two species *L. laudoni* would become a junior synonym, which would have the undesired consequence of making the holotype of this common species a six-armed abnormality.

Sladen's (1879) original description was comprehensive and for the most part accurate, as was the accompanying illustration. His interpretation of the arrangement of ambulacral cover plates is not quite correct, however, as he failed to notice the presence of small occluded plates. Sladen quite correctly recognized the species' distinctness from *Lepidodiscus squamosus* and '*Lepidodiscus*' (*Discocystis*) *kaskaskiensis*.

Genus *POSTIBULLA* Bell, 1976a

Postibulla neglecta sp. nov.

Figs 2, 6, 11

1939 *Lepidodiscus fistulosus* Anderson: 68 (part).

1950 *Anglidiscus fistulosus* (Anderson) Regnéll: 6 (part).

1966 *Anglidiscus fistulosus* (Anderson) Regnéll: U162 (part).

DIAGNOSIS. Agelacrinitid with a domal theca. Ambulacra tall, narrow; ambulacra I–III curve sinistrally, ambulacra IV and V curve dextrally. Cover plates arranged in an alternating series with both large and intercalated plates but precise arrangement not clear. Oral area markedly elongate. Oral cover plates small, undifferentiated from ambulacral cover plates; anterior and posterior series equally developed. Hydropore rise large, separated from oral area; includes one very prominent hydropore plate. Interambulacral plates numerous, squamose and imbricate. Anal pyramid narrow and prominently elevated. Peripheral skirt unknown.

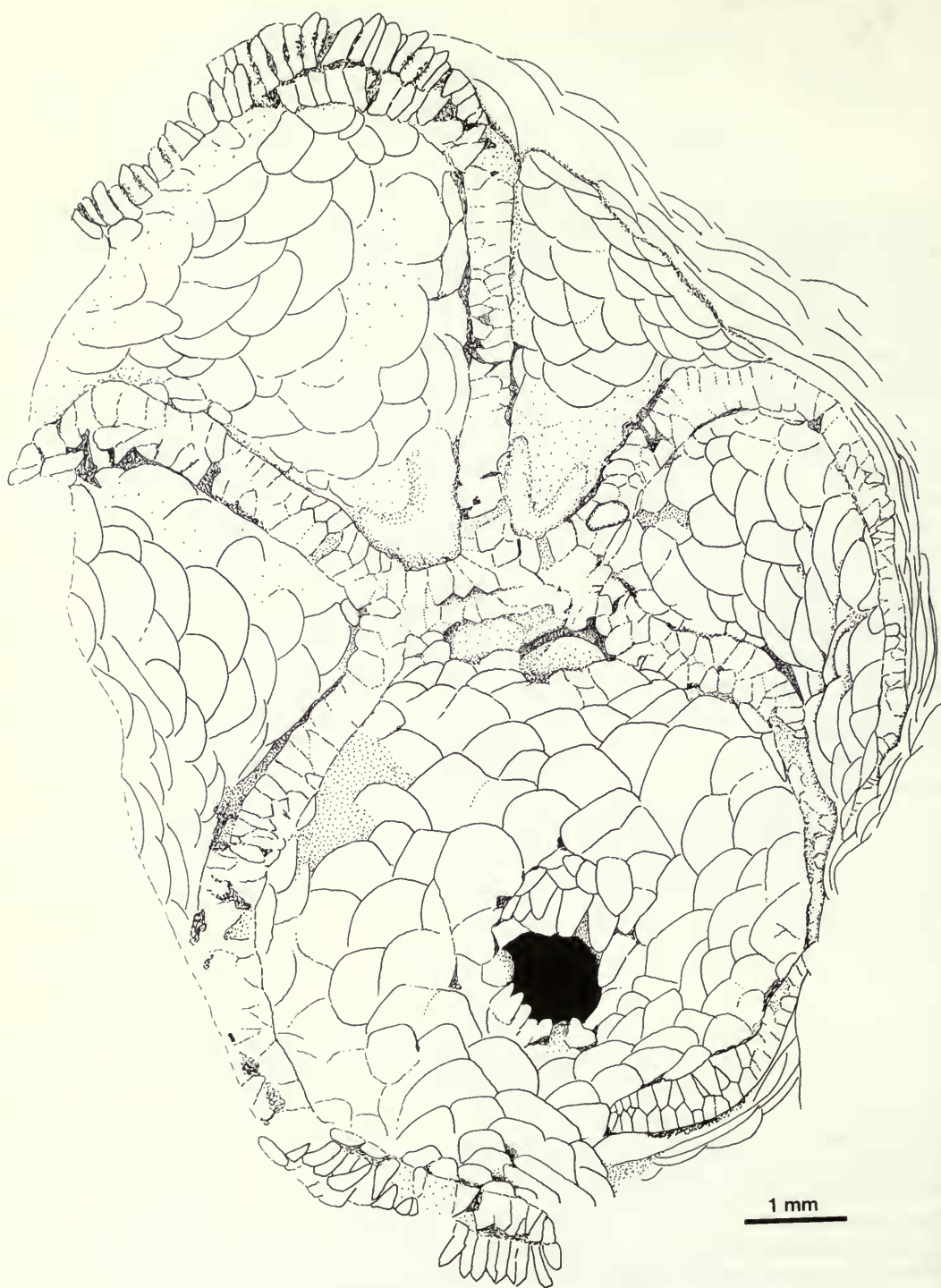


Fig. 11 *Postibulla neglecta* sp. nov. Camera-lucida drawing of the holotype, on IGS no. 60235 (P in Fig. 2). See Fig. 6.

NAME. 'Overlooked'.

MATERIAL. **Holotype**, Institute of Geological Sciences no. 60235, specimen xxvi of Anderson (1939: 70). Paratype, specimen xxx, same slab.

LOCATION AND AGE. Hetton House bore-hole, Northumberland (loc. iii, p. 114). Early Asbian, Dinantian.

DESCRIPTION. Both specimens are 12 to 13 mm in diameter and in life would have been moderately tall and domal in shape; they are preserved in their retracted state. Ambulacra are long and narrow and form prominent ridges over the theca. They are fairly straight adorally but towards the periphery they curve to run parallel with the margin. Ambulacra I–III curve sinistrally whereas ambulacra IV and V curve dextrally. The cover plates are tall and narrow. Where they have fallen outwards each can be seen to have a prominent sagittal ridge on its inner face. The cover plates form a tall steep-sided arch above the ambulacral grooves. Cover plate arrangement is not clear but there appears to be an irregular biseries of larger plates alternating with smaller intercalated plates (Fig. 11). The flooring plates cannot be seen.

The oral area is narrow but laterally extensive so that the ambulacra are in a clear 2–1–2 arrangement. The oral cover plates are continuous with ambulacral cover plates and there are no obviously larger plates. One large plate forms the posterior slope to the oral area opposite ambulacrum III but this I interpret as the most proximal interambulacral plate. An obvious mound to the posterior right-hand side of the oral area forms part of the hydropore structure. There is one large distal hydropore plate clearly separated from the oral area and a smaller proximal hydropore plate. Some of the proximal cover plates of ambulacrum V also border on the hydropore slit.

Interambulacral areas are formed of numerous squamous and imbricate plates. In the most adoral areas of interambulacra 2 and 3 there are crescentic raised areas (Fig. 6, p. 116) which Anderson (1939) interpreted, wrongly in my opinion, as the sites of gonads. The periproct is situated centrally in interambulacrum 5. It is narrow-based and composed of two cycles of rather elongate plates that are wedge-shaped in cross section. In the holotype the anal cone is preserved in its open position.

Beyond the ambulacra, interambulacral plates are vertical and stacked together, showing that the theca was tall in life and has since collapsed. Neither specimen shows the peripheral rim.

DISCUSSION. In erecting the species *Lepidodiscus fistulosus* Anderson (1939) did not realise that individuals belonging to two species (*Lepidodiscus* cf. *squamosus* and *Postibulla neglecta*) were present in his material. His composite reconstruction (1939: fig. 1) bears little resemblance to either species. The reconstruction of soft tissue anatomy given by Anderson (1939: fig. 6) is based on the internal appearance of the holotype of *Postibulla neglecta*. However, apart from the crescentic ridges adjacent to the oral area which he interpreted as the sites of gonads, other structural details cannot be verified.

Both the specimens are preserved upside down and reveal the mould of the external surface. As was discussed for *Lepidodiscus* cf. *squamosus* (p. 118) the specimens are not attached to a recognizable hard ground surface and were probably growing on fronds of a free-standing alga.

The arrangement of ambulacra, the steep-sided, narrow ambulacral ridges and the separation of the hydropore bulge from the oral area clearly place these specimens in the genus *Postibulla*. Five species of *Postibulla* are known, but only two of them come from the Carboniferous (Bell 1976a). These are *P. legrandensis* (Miller & Gurley) and ? *P. jasperensis* (Harker), both from the Kinderhookian, low in the Mississippian. *P. legrandensis* differs from the British species in having three plates forming the posterior rim of the hydropore opening and in having a prominent bulge directly opposite ambulacrum III on the posterior margin of the oral area (Bell 1976a: pl. 40). ? *P. jasperensis* is known only from one small specimen which was placed in this genus only with reservation by Bell (1976a). The cover plates are simple, not irregularly biserial, and the posterior oral protuberance is hardly developed; it is quite unlike the British specimens.

Postibulla neglecta is the youngest species of this genus known.



Genus *STALTICODISCUS* nov.

DIAGNOSIS. A genus of agelacrinitid with tall domal to subclavate theca. Ambulacra I–IV curve sinistrally, ambulacrum V curves dextrally. Ambulacral cover plates arranged in cycles of three, one of which is usually occluded adradially, and with an irregularly zigzag perradial suture. Hydropore rise included in posterior right of oral area (type VI of Kesling, 1960), posterior bounded by two or three plates only. Oral cover plates small, numerous, not differentiated from ambulacral cover plates. Flooring plates uniserial and strongly imbricate. Valvular anal cone consisting of two cycles of plates situated centrally in interambulacrum 5. Interambulacral plates more or less tessellate ventrally but becoming imbricate laterally where they form a cylindrical pedunculate zone. Peripheral skirt present, consisting of some five or six series of plates.

NAME. Greek σταλτικός, 'contracting'.

TYPE SPECIES. *Lepidodiscus milleri* Sharman & Newton, 1892. Monotypic.

DISTRIBUTION AND AGE. From Penruddock, Cumbria and the River Irthing, Northumberland: Early Asbian.

DISCUSSION. This genus is easily distinguished from *Lepidodiscus* on the arrangement of the cover plates. *Lepidodiscus* has cover plates that are arranged in cycles of six, usually with three larger plates and three smaller occluded plates (Fig. 10), whereas *Stalticodiscus* has cover plates arranged in cycles of three with two larger plates and a smaller, often occluded plate. *Discocystis*, like *Stalticodiscus*, has its cover plates arranged in cycles of three, or occasionally in cycles of four, but here the perradial edge of the cover plates is obviously serrated, suggesting that there are 'multiple intra-ambulacral extensions on the ambulacral tunnel surfaces of the cover plates' (Bell 1976a: 251). Furthermore, *Discocystis* has polygonal, tessellate plating in the interambulacral areas and a downwardly constricting pedunculate zone of subrectangular plates clearly demarcated from the ventral surface. In *Stalticodiscus*, interambulacral plating is, at most, sub-tessellate and the pedunculate zone is neither clearly demarcated from the ventral surface, nor downwardly tapering. The flooring plates of *Discocystis* abut along vertical sutures, whereas those of *Stalticodiscus* are strongly imbricate. For these reasons *Stalticodiscus* and *Discocystis*, though clearly closely related, are separated as distinct genera.

Stalticodiscus milleri (Sharman & Newton, 1892)

Figs 12–51

1892 *Lepidodiscus milleri* Sharman & Newton: 150; pl. 2, figs 1–5.

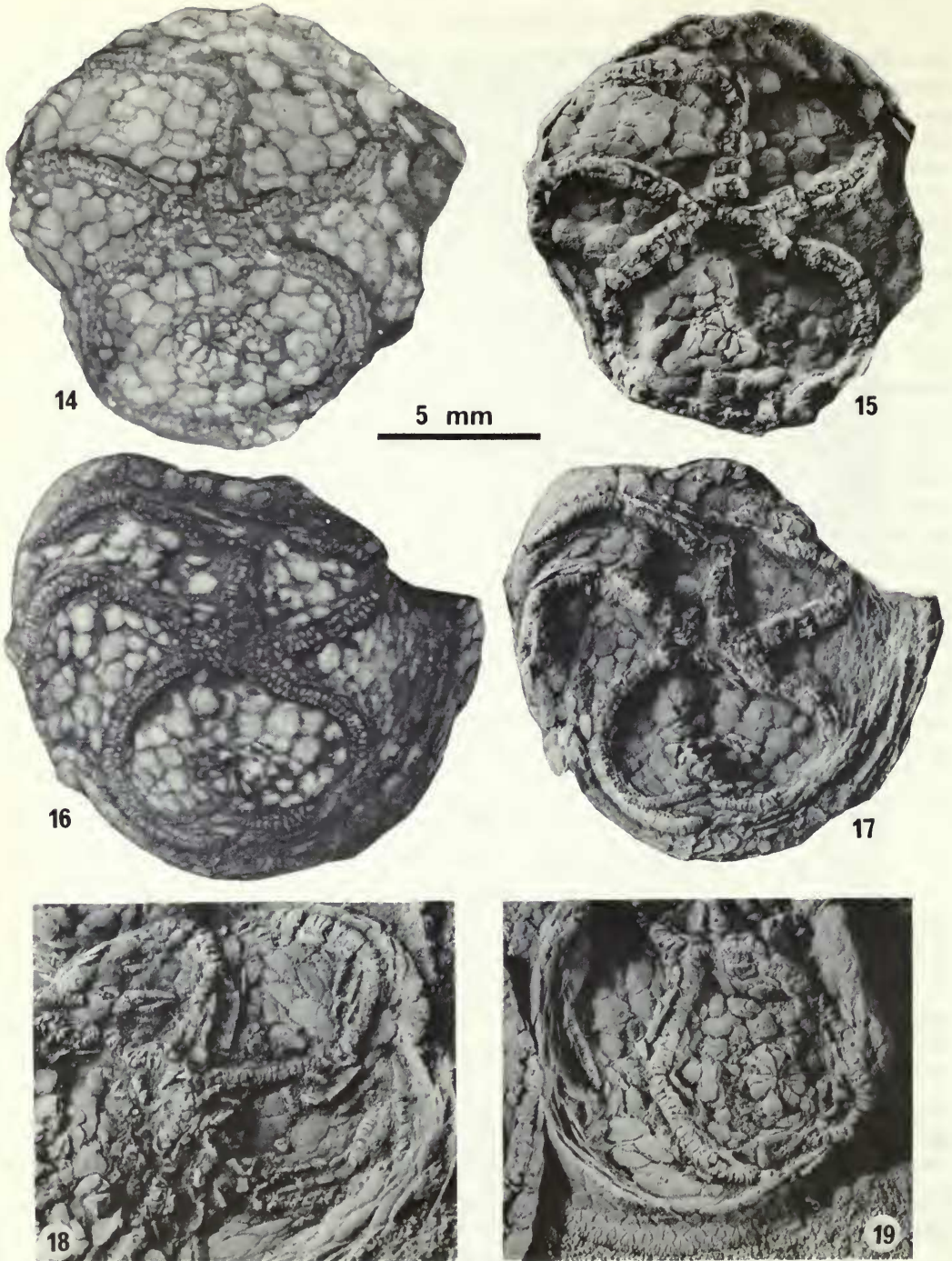
1936 *Lepidodiscus milleri* Sharman & Newton; Bassler: 20; pl. 7, fig. 7.

DIAGNOSIS. A subclavate species of *Stalticodiscus* up to 15 mm in diameter and 30 mm or so in height. Interambulacral plating sub-tessellate ventrally, imbricate laterally. Periproct situated centrally in interambulacrum 5. Ambulacra I and V just overlapping behind the periproct in adults.

MATERIAL. Holotype, Institute of Geological Sciences no. 7662. Other specimens, IGS 25105, also many hundreds of individuals from Penruddock, British Museum (Natural History) Palaeontology Dept nos E29878–925.

LOCATION AND AGE. The holotype IGS 7662 and IGS 25105 come from the Millerhill limestone, Early Asbian, of the River Irthing, Northumberland. The holotype comes from near Waterhead

Figs 12–13 *Stalticodiscus milleri* (Sharman & Newton), BM(NH) no. E29878. Fig. 12, a limestone concretion encrusted by adults some in extended posture. Notice that all are aligned with their anterior towards the right or top right. Fig. 13, an enlarged view of the two fully extended individuals seen in Fig. 12, showing the imbricate pedunculate zone. On collapse the theca has been compressed onto its own elevated peripheral rim to produce the circular impression towards the base. Scale bar = 5 mm. All specimens whitened with ammonium chloride sublimate.



Figs 14–19 *Stalticodiscus milleri* (Sharman & Newton). Figs 14–15, BM(NH) no. E29884: Fig. 14 under xylene, Fig. 15 whitened with ammonium chloride sublimate. Figs 16–17, BM(NH) no. E29889: Fig. 16 under xylene, Fig. 17 whitened with ammonium chloride sublimate. Fig. 18, BM(NH) no. E29885. Oral surface with cover plates partially lost to reveal uniserial flooring plate arrangement. Fig. 19, BM(NH) no. 29888. Posterior half of the specimen showing the peripheral rim plating and the arrangement of plates forming the periproct. Note the large hydropore bulge to the posterior right of the oral area. Scale bar 5 mm.

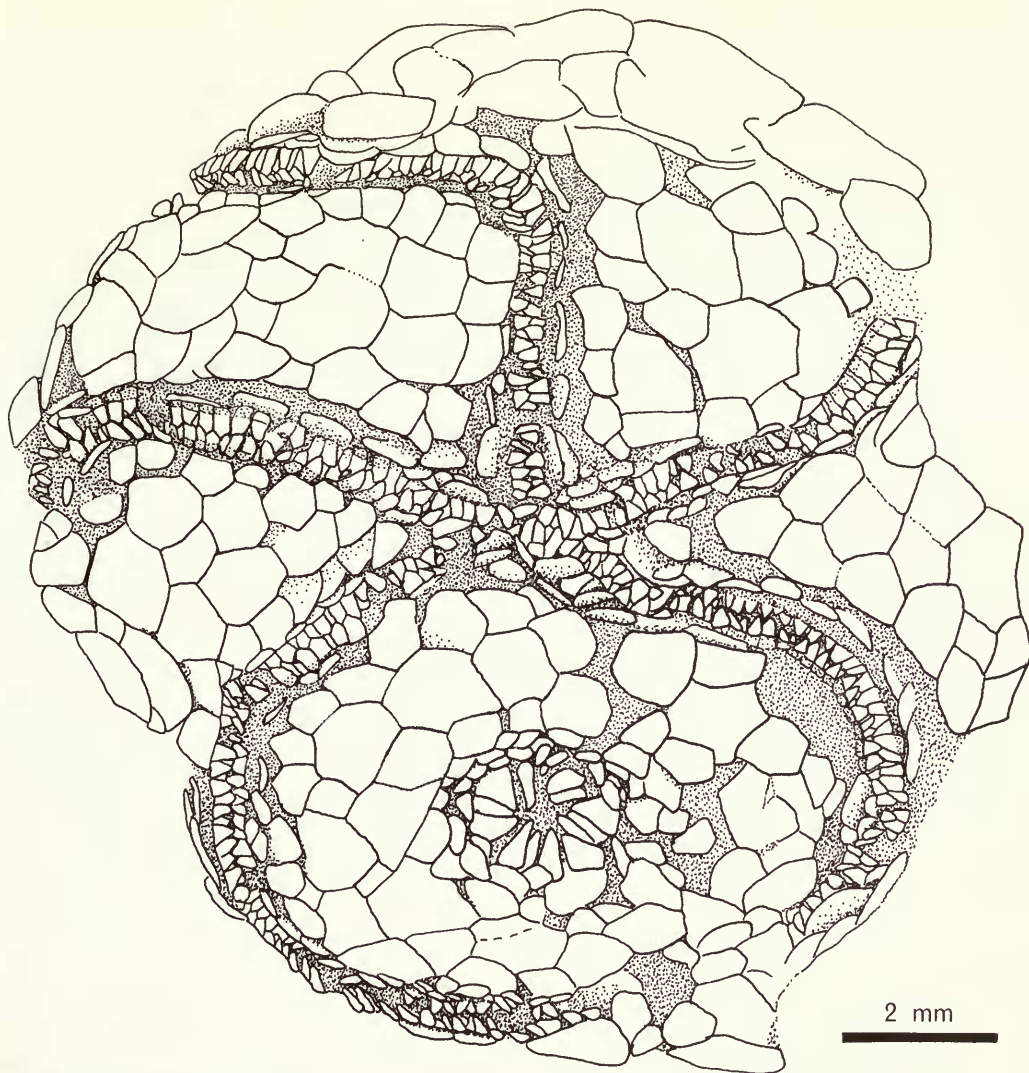


Fig. 20 *Stalticodiscus milleri* (Sharman & Newton), BM(NH) no. E29884. Camera-lucida drawing.

(loc. i, p. 114), the other from near Lampert (loc. ii). Many hundreds of individuals encrusting limestone concretions have also been collected from Penruddock, Cumbria (loc. v) and are also Early Asbian in age.

DESCRIPTION. Until recently, only two poorly-preserved specimens of this species were known. The discovery of colonies totalling many hundreds of individuals, ranging in size from less than 0.5 mm to more than 15 mm in diameter, at Penruddock has provided an abundance of well-preserved material on which to base this description.

Mature individuals are subclavate in shape when fully extended (Fig. 13) but are usually preserved in a contracted posture with the lateral peduncular zone telescoped together just inside the marginal ring (Fig. 27). When fully extended the theca is twice as tall as it is broad, and it tapers slightly towards its attachment base. The ambulacra extend down less than half the height of the theca. Juveniles are less elevated and generally domal in shape. The pedunculate zone only starts to become obviously developed once individuals have reached a diameter of about 8 to 10 mm. The peripheral rim is usually circular in outline but may be distorted if the individual is attached to an uneven surface or a relatively small object such as a shell.

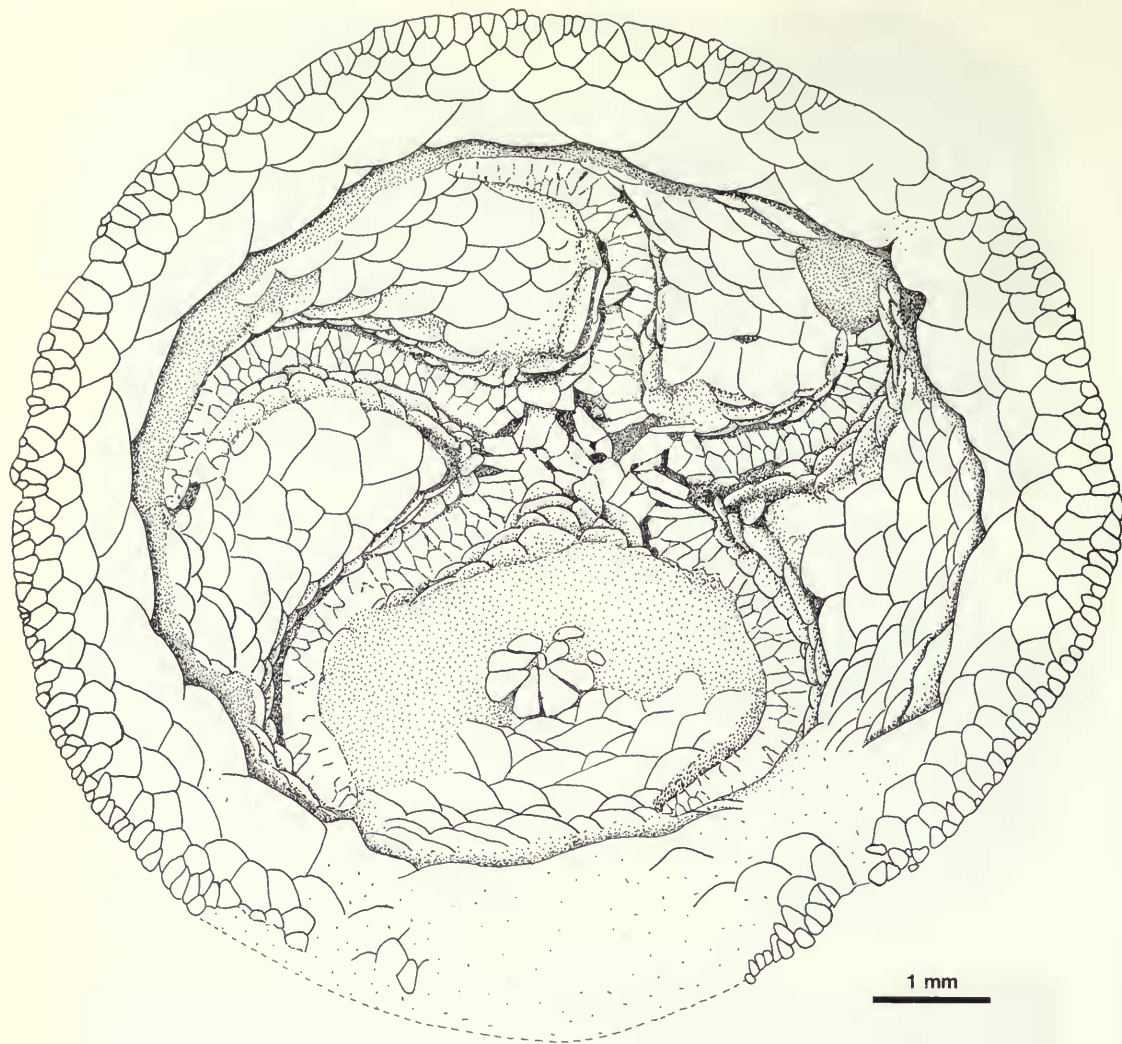
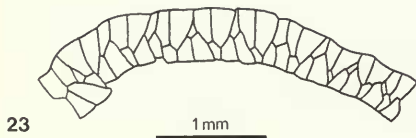
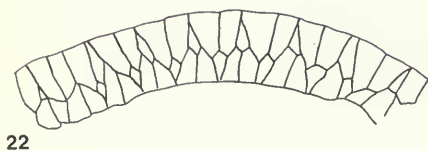


Fig. 21 *Stalticodiscus milleri* (Sharman & Newton), IGS no. 7662, holotype. Camera-lucida drawing. See Fig. 25.



Figs 22–23 Camera-lucida drawings of ambulacral cover plate arrangement in *Stalticodiscus milleri* (Sharman & Newton), approximately mid-length along the ambulacrum. Fig. 22 BM(NH) no. E29571; Fig. 23 BM(NH) no. E29885.

Ambulacra form prominent ridges over the theca, and are only moderately long. Ambulacra I–IV curve sinistrally, ambulacrum V curves dextrally. The two posterior ambulacra curve round to encircle the periproct, but it is only in the largest individuals that the two ambulacra more or less meet posteriorly behind the periproct. These ambulacra may just overlap at the anterior–posterior mid-line. Ambulacra maintain a uniform breadth along most of their length, tapering only at their distal tip. Cover plates are arranged in irregular cycles of three, usually consisting of two larger plates and a smaller, often occluded plate (Figs 22, 23). Proximally, near the oral area plating becomes more irregular. Near the distal tip (Fig. 34) the perradial suture is obviously zigzagged, but over most of the ambulacrum this suture is much more irregular in its path (Fig. 30, p. 131).

Cover plate arrangement continues across the oral area without obvious distinction from ambulacral areas (Figs 30–32). A few plates are slightly larger than any found in the ambulacra, but there are no enlarged primary oral plates. Two shared cover plates situated at the fork between paired lateral ambulacra are usually conspicuous. The arrangement of plates in the oral area is not fixed, and in the large number of specimens available much variation exists, particularly in the presence or absence of small occluded plates.

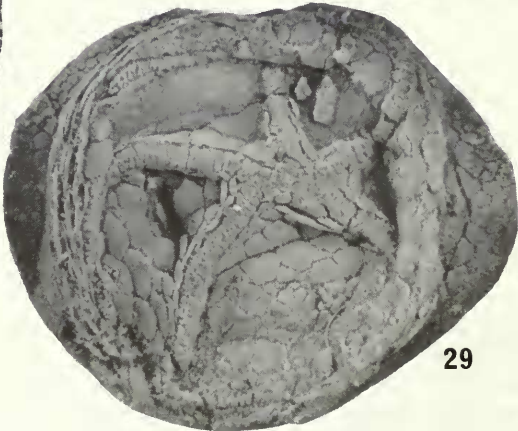
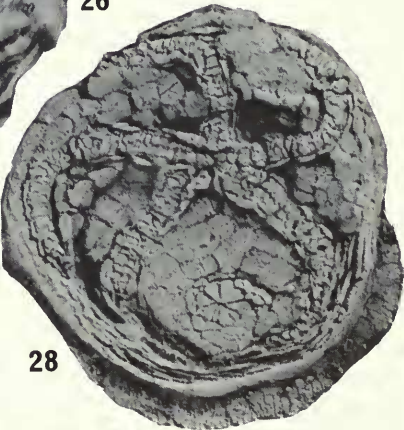
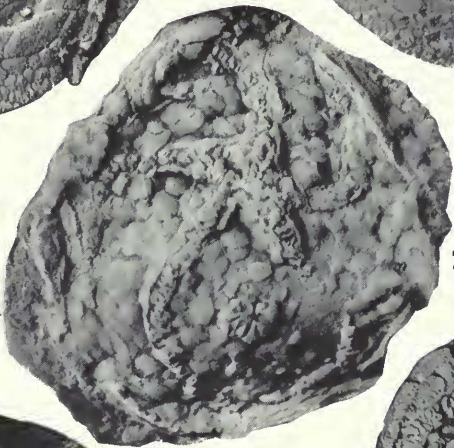
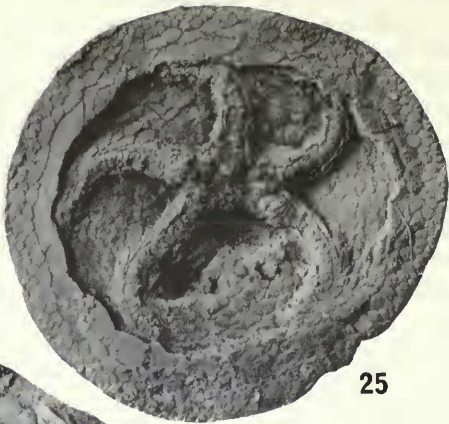
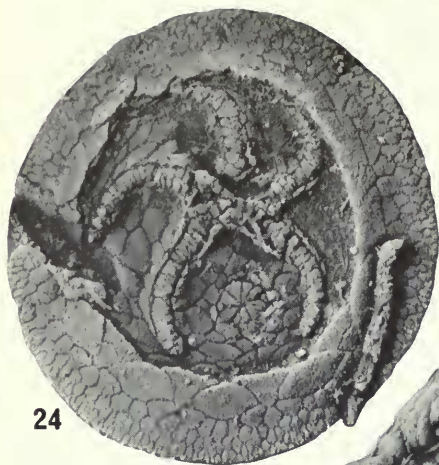
Ambulacral flooring plates are uniserial and imbricate. Each plate has a large distal tongue which overlaps the base of the adjacent flooring plate (Figs 38–40). This imbrication is not immediately apparent from an external view of an ambulacrum stripped of its cover plates (Fig. 18). Flooring plates have a deep, U-shaped channel which shows no signs of muscle attachment scars or grooves for soft-tissue tracts. Although the floor of this channel is relatively thick, the lateral walls are thinner. There is a distinct bulge on each side approximately half-way along (Figs 38–40). The functional significance of this structure is unknown but it is present in at least some other agelacrinitid edrioasteroids (Bell 1976a). Cover plates rest on top of the lateral walls of the flooring plates but there appears to be no obvious structural modification to accommodate them. Adradially the cover plates have a small intrathecal extension which overlaps the flooring plate to extend beneath adjacent interambulacral plating (exposed in areas shown in Figs 31 and 34). The structure of the oral frame is unknown but is presumably like that of other agelacrinitids.

The hydropore structure forms a distinct bulge to the right posterior of the oral area (Figs 27–31). It is bounded by several cover plates of ambulacrum V anteriorly and by two large hydropore plates to the posterior. The hydropore bulge matches a type VI hydropore of Kesling (1960).

Interambulacral areas are broad. On the ventral surface the plating is sub-tesselate (Figs 14–17) but laterally the interambulacral plates imbricate to form a pedunculate zone. Interambulacral plates are thin with bevelled edges. The outer surface is covered by a dense stereom layer with a granular surface (Figs 31–36). The bulk of the plate is thickened with a coarse labyrinthic stereom but there are a couple of retiform stereom layers near the outer surface (Figs 37, 41). Within each interambulacrum larger plates are found towards the centre whereas smaller plates border the ambulacra and surround the periproct. The imbricate plating making up the pedunculate zone is arranged irregularly (Fig. 13). This zone could be expanded and contracted like a telescope by varying the amount of overlap of the constituent plates. Presumably there were both meridional and circumferential muscle layers underlying the thecal plating to bring about this change in shape.

The periproct lies centrally in the posterior interambulacrum. It forms a well-defined anal cone composed of two cycles of plates. The primary cycle consists of some eight large triangular plates. Within this cycle, and largely hidden from sight, is a second cycle of smaller plates lying distally nestled between primary anal cone plates. When the anal cone is undisrupted only the very tips of these secondary plates can be seen at the apex of the cone (Fig. 30). In large specimens the primary and secondary plates alternate.

The peripheral rim is circular in outline and forms a cohesive framework. It consists of some five rows of plates which become progressively smaller towards the margin (Figs 19, 24, 36). The innermost plates alternate, every other plate being set behind. These plates have an expanded base which is set firmly on the substratum. The base is marked by a series of radial ridges and



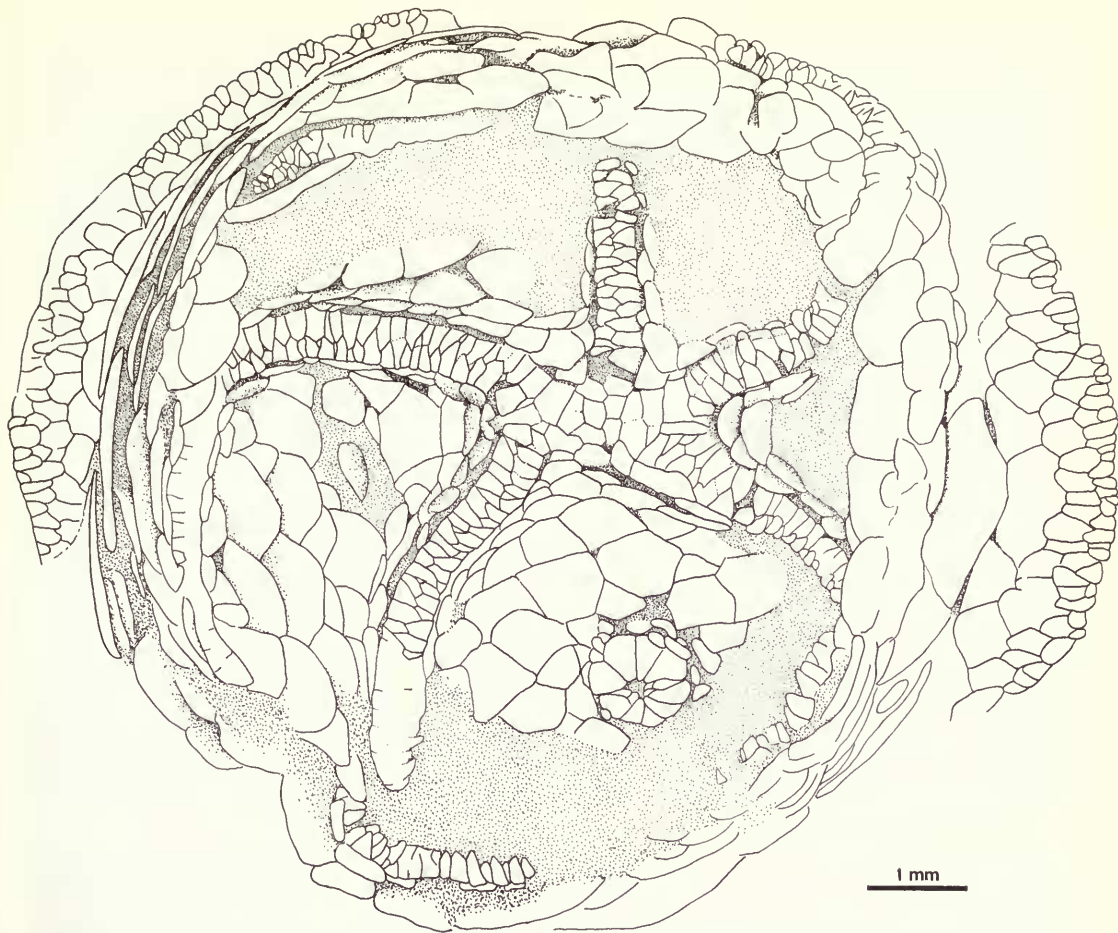
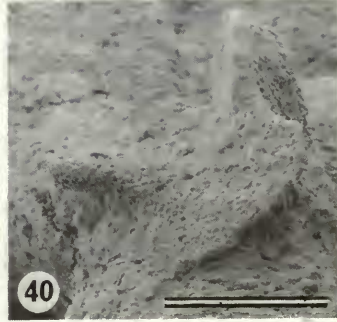
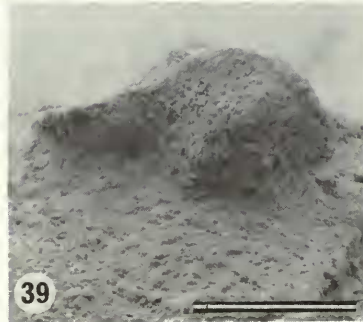
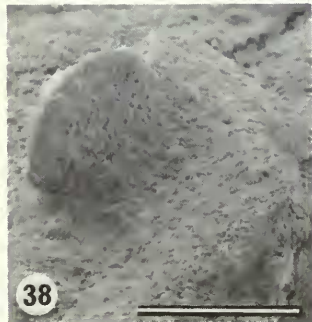
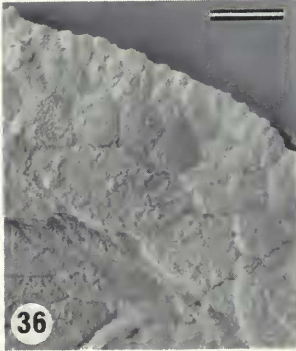
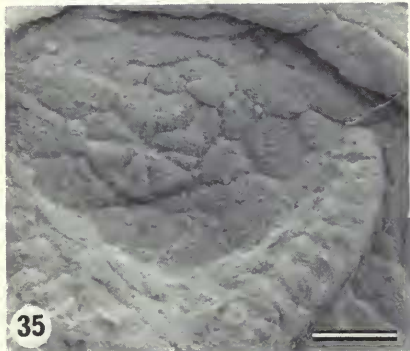
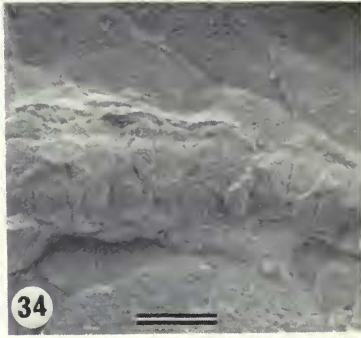
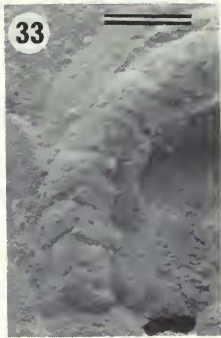
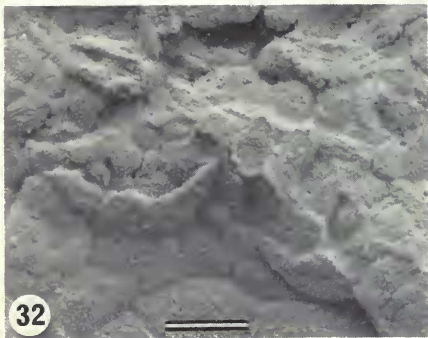


Fig. 30 *Stalticodiscus milleri* (Sharman & Newton), BM(NH) no. E29887. Camera-lucida drawing showing the cover plate arrangement in the oral area. See Fig. 29.

grooves which presumably played some role in adhesion. The more distal plates of the peripheral rim are tessellate and also have radial ridges on their lower surfaces, but these are less well developed.

GROWTH. The changes that take place during the growth of isorophid edrioasterioids have been described by Bell (1976b). Bell was able to study ontogeny in all the isorophid families save for the Agelacrinitidae. The large number of juvenile *Stalticodiscus milleri* now available permits the first detailed description of growth in a member of the Agelacrinitidae. In this study, small individuals were studied using a scanning electron microscope and a representative growth series is shown in Figs 42–51.

Figs 24–29 *Stalticodiscus milleri* (Sharman & Newton). Fig. 24, BM(NH) no. E29886, 7 mm diameter juvenile, $\times 8$. Fig. 25, IGS no. 7662, holotype from the River Irthing, $\times 6$; see Fig. 21. Fig. 26, IGS no. 25105, the other specimen mentioned by Sharman & Newton (1892) as coming from the River Irthing, $\times 6$. Fig. 27, BM(NH) no. E29879, a large specimen; anterior to the right showing the well-developed zone of imbricate plates, $\times 6$. Fig. 28, BM(NH) no. E29883, small adult from Penruddock with the same diameter as the holotype, $\times 6$. Fig. 29, BM(NH) no. E29887, specimen with a well-preserved oral area, $\times 6$; see Fig. 30. All specimens whitened with ammonium chloride sublimate.



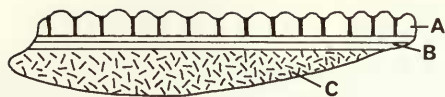
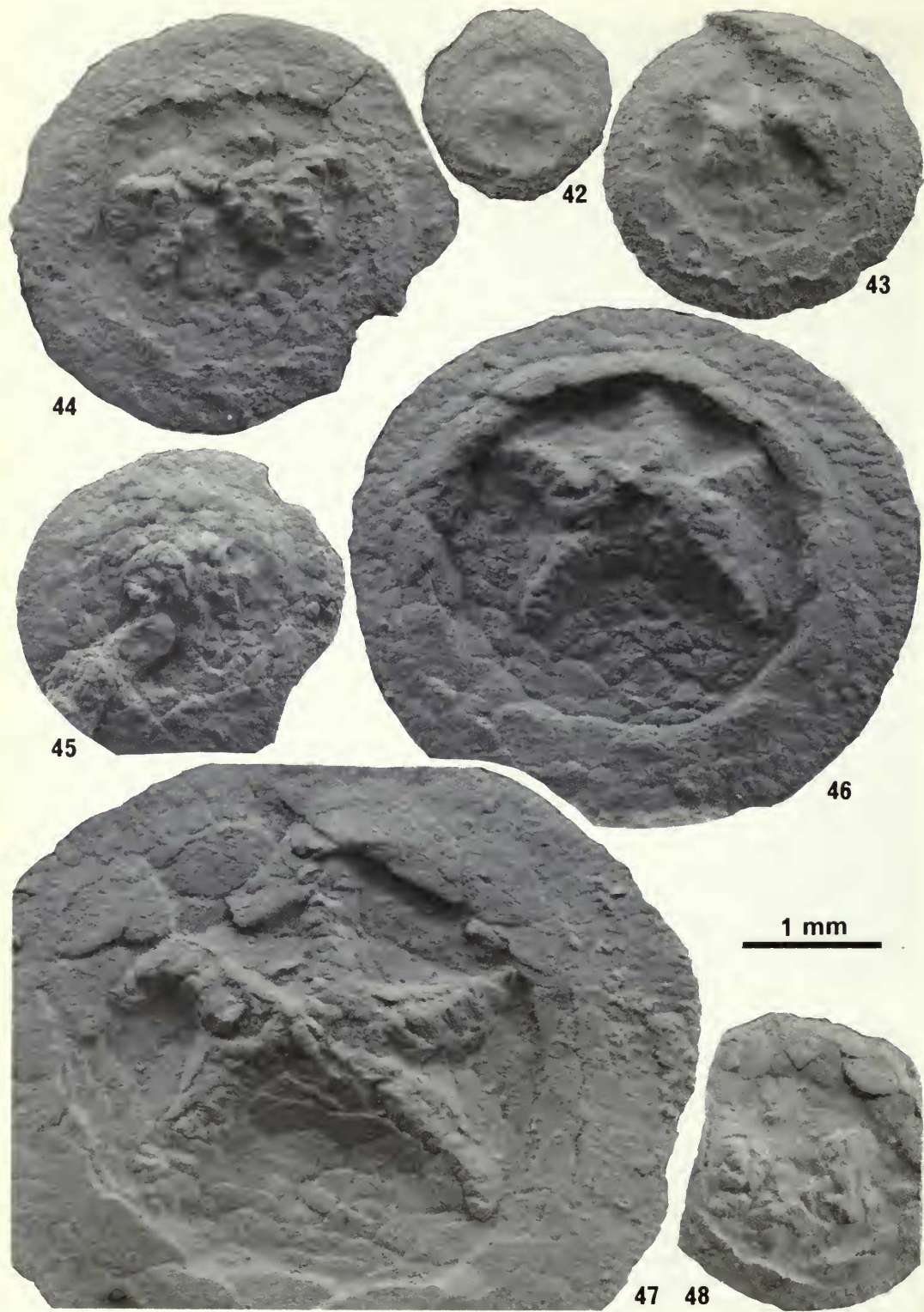


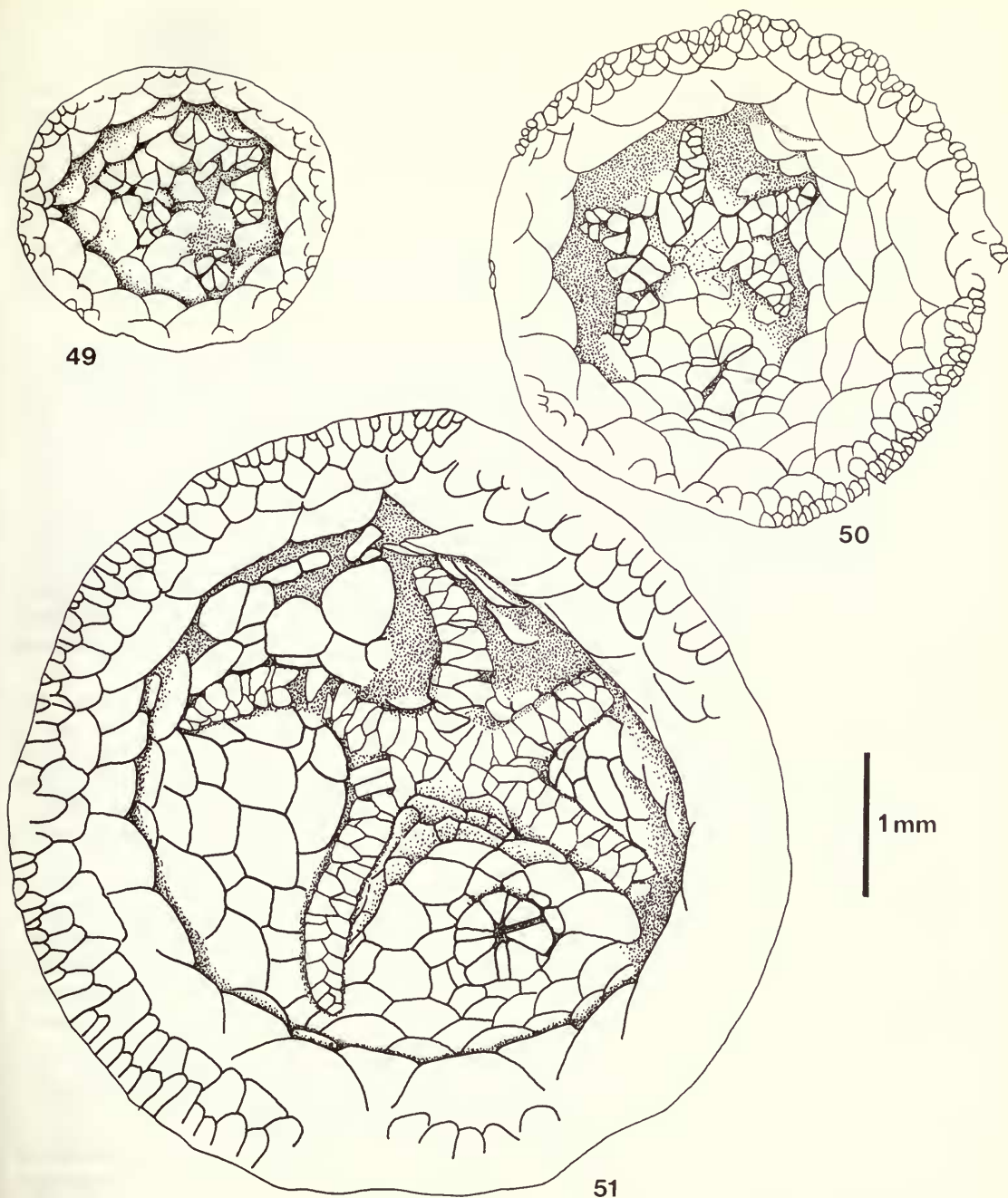
Fig. 41 Reconstructed cross section through an interambulacral plate of *Stalticodiscus milleri* (Sharman & Newton). A, outer dense, perforate stereom layer with granular surface. B, thin middle layer of laminar stereom. C, thick inner layer of coarse labyrinthine stereom.

As in all isorophids, the peripheral rim is much more prominent in juveniles than it is in adults. The central disc is only 55% of the diameter of the theca at about 1 mm diameter, approximately 60% at 2–3 mm diameter, 65–70% at 4–7 mm diameter and reaches a little less than 80% by 12–15 mm diameter. At 1 mm diameter the peripheral rim consists of just two rows of plates but the number of rows increases progressively to a total of five by about 7–8 mm diameter (Fig. 36). Bell (1976b) reported that new peripheral rim plate cycles were added by insertion between the first two cycles of plates. I could find no evidence that this took place in *S. milleri*, where new plate cycles appear to have been added at the outer edge. The inner alternating cycle of large peripheral rim plates do not form an obvious palisade until about 2 mm diameter. New plates continue to be added to the inner cycle of plates until approximately 6 mm diameter, after which time growth continues by plate enlargement only.

Within the disc, plating is poorly differentiated to start with. At 1 mm diameter the disc is dominated by an elongate mound (Fig. 42) but at this size it is impossible to distinguish individual plates. Presumably at this stage ambulacral cover plates exist but are extremely thin and poorly preserved. By 2 mm diameter the ambulacra have started to differentiate and there are five small but distinct points to the elongate oral area. Cover plate arrangement can be made out and there are four slightly larger cover plates in the oral area; two anterior ones situated at the junction of ambulacra II and III, and ambulacra III and IV, and two posterior ones between ambulacra I and V. The large posterior right oral cover plate eventually becomes the hydropore plate. At 2 mm diameter the rudimentary ambulacra consist of just two or three cover plates per column, but by 4 mm diameter the ambulacra are obviously developed and consist of some six to eight cover plates per column. Ambulacra are still more or less straight. The ambulacra start to curve gently by about 5.5 mm diameter (by which time there are 12 to 14 cover plates per column) and, for the first time, small occluded cover plates become apparent. The cyclical arrangement of cover plates is fully developed by 7 or 9 mm diameter. At 7 mm diameter the anterior and two lateral ambulacra are more or less prominently curved, but the posterior two ambulacra are only weakly curved and their tips only slightly convergent. By 13 mm diameter the posterior two ambulacra have grown to more or less meet behind the periproct and in larger specimens the tips of the ambulacra may overlap very slightly. New ambulacral cover plates are added distally at the tips of growing ambulacra.

Figs 31–40 Scanning electron micrographs of *Stalticodiscus milleri* (Sharman & Newton) from Penruddock. All BM(NH) numbers. Fig. 31, E29907, oral area of a 13 mm diameter individual showing a clear hydropore bulge. Fig. 32, E29908, individual 10 mm in diameter showing a rather different arrangement of oral cover plates. Fig. 33, E29915, the distal part of ambulacrum II in an 8 mm diameter individual, showing the early appearance of secondary (occluded) cover plates near the distal tip. Fig. 34, E29908, the adoral part of ambulacrum V in a 10 mm diameter specimen showing the cyclical arrangement of cover plates and the zigzag perradial suture. Fig. 35, E29897, periproct in a 5.5 mm diameter individual with both primary and secondary cycles of periproctal plates; see Fig. 51. Fig. 36, E29895, the fully formed peripheral rim of plates in an individual 6.5 mm in diameter. Fig. 37, E29921, a large interambulacral plate seen from the inside with an extensive zone of labyrinthine stereom and a more marginal laminar stereom. Figs 38–40, E29918, ambulacral flooring plate: Fig. 38, external (distal edge to top of photomicrograph); Fig. 39, lateral (distal edge to left of photomicrograph); Fig. 40, front view of distal face. Scale bar = 0.5 mm.





Figs 49–51 Camera-lucida drawings of juvenile *Stalticodiscus milleri* (Sharman & Newton). All BM(NH) numbers. Fig. 49, E29893, see Fig. 48; Fig. 50, E29885; Fig. 51, E29897, shown inverted in Fig. 35, p. 132.

Figs 42–48 Scanning electron micrographs of juvenile *Stalticodiscus milleri* (Sharman & Newton), all to the same scale. All BM(NH) numbers. Fig. 42, E29899; Fig. 43, E29898; Fig. 44, E29911; Fig. 45, E29917; Fig. 46, E29901; Fig. 47, E29894; Fig. 48, E29893, see Fig. 49.

Interambulacral areas are minimal at 1 mm diameter and no interambulacral plates can be made out at this size. Interambulacral plates first become apparent at about 2 mm diameter. As growth proceeds, interambulacral areas become progressively larger relative to the disc, and new plates are added immediately inside the peripheral rim as well as adjacent to the ambulacra and periproct. By about 8 mm diameter the full complement of ventral interambulacral plates are present and it is at about this size that the pedunculate zone starts to develop. At 7 mm diameter the theca is still low and domal in profile but around 8 to 10 mm diameter a zone of imbricate plating starts to form between the edge of the ventral surface and the peripheral rim. This pedunculate zone is fully developed by 12 to 15 mm diameter, but at what stage it starts to develop varies. For example, it is poorly developed in the holotype, which is 9 mm in diameter, but most Penruddock specimens have a fairly well developed zone of imbricate plates by this diameter. Presumably environmental factors influenced the size at which the pedunculate zone formed.

The periproct does not appear until about 2 mm diameter, at which stage it is a circular area composed of some four triangular plates set flush with the interambulacral plates. By 3 mm diameter the periproct has become elevated and forms a conical structure, and by 4 mm diameter the full complement of primary cycle periproctal plates is present. At about 6 mm diameter the first of the secondary cycle of periproctal plates appears.

Plating arrangement over the oral area is in its final form by about 6 mm diameter. The hydropore cover plate appears very early and is present by 2 mm diameter. It continues to enlarge throughout the early growth stages. The hydropore bulge to the posterior right of the oral area is absent at 4 mm diameter, starts to form at about 5 to 6 mm diameter and is prominent by 7 mm diameter. This probably coincides with the onset of gonadal development, as the so-called hydropore passageway is probably a combined hydropore/gonopore. The appearance of the hydropore bulge would then be the best morphological change on which to distinguish juveniles from sexually mature adults.

The ontogenetic changes that take place in *S. milleri* are in close agreement with the development of other isorophids reported by Bell (1976b). There are, however, two minor differences. Firstly, I could find no evidence that plates of the peripheral rim were added by insertion: here addition took place at the outer edge. Secondly, the cover plates of the oral area are hardly differentiated from ambulacral cover plates even during the early ontogenetic stages. This quite obviously reflects the fact that in adult agelacrinitids there are no enlarged oral cover plates such as are found in other families.

DISCUSSION. The holotype of '*Lepidodiscus*' *milleri* is not well preserved and comes from a slightly higher horizon in the Early Asbian than does the Penruddock material. The holotype differs slightly from the Penruddock material in that it has a more juvenile appearance than would be expected for its size. At 9 mm diameter it has the appearance of a 7 mm diameter Penruddock specimen, lacking the pedunculate zone development and strong ambulacral curvature expected by this size. As the only difference between the holotype and the Penruddock specimens is one of developmental rate, all are placed within the same species. The rate of ontogenetic development is likely to be influenced by environmental factors such as the hydrodynamic regime or substratum availability and intraspecific competition.

The Penruddock population of *S. milleri* was killed by a sudden influx of sediment and the animals are preserved in various stages of contraction (compare Figs 13 and 27). Specimens that are not fully contracted are generally preserved lying over to one side (see, for example, Fig. 12), flattened by the influx of sediment that killed them. The direction in which they have fallen presumably coincides with the prevailing current direction at death. The fully contracted specimens have collapsed further following compaction and probably had a low domal profile in life. Presumably contraction and expansion were effected by circumferential and longitudinal muscle layers immediately beneath the thecal plating. Adults were not permanently cemented to the substratum but could swivel, much like sea anenomes. Orientation is more or less random on boulders settled by juveniles. However, once the pedunculate zone had begun to form, orientation obviously became more important. For example, on BM(NH) nos E29878–82 (one

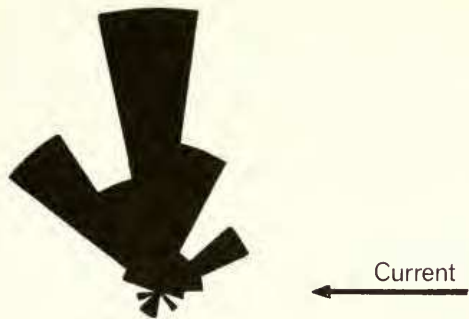


Fig. 52 Rose diagram showing the orientation (anterior of the anterior-posterior axis) for 55 adults encrusting one limestone concretion. The current arrow shows the direction in which the sediment that smothered the colony was brought in.

boulder), all adults are orientated in the same direction with their anterior ambulacra facing more or less at right angles to the direction of sediment input that killed them (Fig. 12). A strong orientation is found on many other boulders (Fig. 52), though not on all. The direction of sediment input need not correspond to the direction of the prevailing current. However, Foerste (1914) found precisely the same orientation in populations of *Carneyella pilea*. Here, as in *S. milleri*, it is ambulacra IV and V that face towards the direction of sediment influx. The fact that in both species the anterior-posterior axis was orientated at right angles to the direction of the current that smothered them suggests that this was indeed the orientation that they adopted in currents. It also suggests that these isorophids were living in a tidal regime with bimodal currents, since in unidirectional flow one would expect the anterior to face into the current so that the periproct was positioned downstream of the mouth.

Acknowledgements

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